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Respiratory frequency, total evaporative water loss and heart rate in the Kinkajou (*Potos flavus* Schreber)¹

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Abstract

Studied heart rate, respiratory frequency and total evaporative water loss in kinkajou (*Potos flavus*). Mean rectal temperature could be regulated within 35.8–37.3 °C at ambient temperatures from 10–33 °C; when exposed to 35 °C it rose to 38.6 °C. Oxygen consumption was lowest between 23–33 °C (basal metabolic rate 0.34 ml O₂/g·h); this is only 71 % of the expected mass-specific value. At ambient temperatures below the thermoneutral zone O₂-uptake increased following the regression line: $Y \text{ (ml O}_2\text{/g}\cdot\text{h)} = 0.698 - 0.015 T_a \text{ (}^\circ\text{C)}$. Mean resting heart rate was lowest between 23–28 °C with about 78 beats/min; a minimal rate was measured at 23 °C with 68 beats/min. The mean oxygen pulse was at 170–182 µl/beat at temperatures from 28–35 °C; it rose to 245 µl/beat at T_a = 10 °C. Mean breathing rates during sleep were at 12 breaths/min when exposed to temperatures from 23–30 °C. Lower temperatures led to a slight increase only. At T_a = 33 °C respiratory frequency rose to 29–80 breaths/min and at 35 °C panting started when the rectal temperature had reached a threshold value between 37.5–38.1 °C. Maximal panting rates were at 480 breaths/min. Between 10–25 °C mean total evaporative water loss was at 0.37–0.46 ml/kg·h. During continuous panting it increased to about 1.5 ml/kg·h. However, heat dissipation through evaporative pathways was low: At T_a = 33 °C only about 30 % of the endogenous heat production were dissipated by evaporation and this ratio even diminished during panting due to the simultaneous increase of oxygen uptake.

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Introduction

The mainly frugivorous kinkajous are strictly nocturnal members of the family Procyonidae. They live in rain forests from Southern Mexico to Brazil, where they belong to the fauna of the middle-jungle (POGLAYEN-NEUWALL 1962). In this zone, at a height of 5–25 m, the air temperature is usually at about 25 °C and increases to above 30 °C only in direct sunshine (ALLEE 1926).

In a previous study it could be shown that kinkajous have a low basal metabolic rate, only about 65–70 % of the mass-specific value (MÜLLER and KULZER 1977). The reduced basal heat production can be regarded as an energy saving adaptation favoured by the stable climatic conditions. Additionally, McNAB (1978) pointed to the possible influence of arboreal and frugivorous-omnivorous habits on the basal metabolism of mammals.

It was the aim of this study to find out if the relatively small climatic variations in the environment of the kinkajous have also affected their thermoregulatory abilities. For this purpose we measured heart rate, total evaporative water loss and respiratory frequency at ambient temperatures from 10–35 °C. In addition we tested the effects of different relative humidities in the surrounding air on these parameters.

Materials and methods

For the experiments we used a couple of kinkajous which had been purchased in Columbia in 1975. Since that time the animals have been kept in our laboratory in a wire cage (180 × 130 × 180 cm); they were exposed to a L:D-cycle of 12:12, with the D-phase from 19–7 hr. Before and during the investigations the kinkajous were acclimated to a room temperature of 25 ± 1 °C and a relative humidity of 60 ± 10 %. Food consisted mainly of bananas, apples, carrots, lettuce and chickens; twice a week a pap of gruel, eggs, bananas and honey was given, which had been vitaminized with Protovita. Drinking water was always available. The mean body mass of the animals during the investigations was 2400 g in the male and 2800 g in the female.

Exposure to the various ambient temperatures (T_a) usually lasted 5–6 hours; at $T_a = 35$ °C, however, the experiments were stopped after 2–4 hours, depending on the state of excitement of the kinkajous. All measurements were done during the resting period from 9–16 hr. With the exception of high ambient temperatures the fasting animals quickly fell asleep after having been placed in the respiration box (perspex; dimensions 33 × 39 × 32 cm). The box stood in a temperature controlled cabinet (Ehret), where ambient temperature could be regulated to ± 1 °C. A schematic drawing of the experimental arrangement is given in Figure 1.

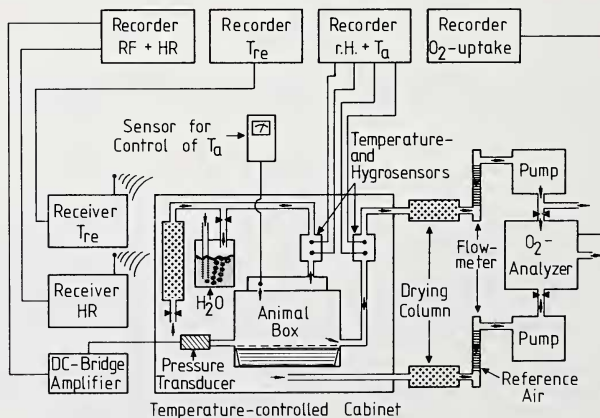


Fig. 1. Schematic drawing of the experimental arrangement. Faeces and urine were caught under paraffin oil. Arrows indicate direction of air flow

Oxygen consumption was measured in an open system with a Beckman G2 oxygen analyzer. Air was drawn through the respiratory box at constant rates from 100–341 l/h (STPD); the air flow was continuously controlled with a flowmeter (ROTA). Oxygen uptake was calculated as mean value after an equilibration time of 1–2 hours; all gas volumes are corrected to STPD.

Rectal temperatures (T_{re}) were determined after the end of each experiment at a depth of 8 cm with a thermistor (Testotherm digital 2500; accuracy ± 0.1 °C). During several experiments at high ambient temperatures, T_{re} was also monitored continuously with a temperature transmitter which had been inserted into the rectum.

Heart rates were measured by telemetry as described elsewhere (MÜLLER et al. 1979).

Total evaporative water losses were determined by use of two hygrosensors which measured the relative humidity of the air entering and leaving the animal box; the method has been described earlier (MÜLLER and JAKSCHE 1980). Different relative humidities of the air entering the animal box were produced by mixing pre-dried air with air saturated with water vapour. Respiratory frequencies were measured by whole body plethysmography using a pressure transducer (Statham Lab., P23BB; range 0–50 mm Hg).

Results

Rectal temperature (T_{re})

The mean rectal temperatures at the end of the experimental runs varied from 35.8 °C ($T_a = 10$ °C) to 38.6 °C ($T_a = 35$ °C) (Fig. 2). At ambient temperatures from 10–25 °C T_{re} was usually lower in the male.

Recording T_{re} by telemetry revealed that at $T_a = 35$ °C T_{re} rose steadily within the first two hours to about 38 °C. If the kinkajous remained quiet the rise of T_{re} then gradually attenuated. In most cases, however, the animals became restless and T_{re} quickly increased to above 39 °C. Then the experiments were stopped to spare the animals.

Oxygen consumption ($\dot{V}O_2$)

Oxygen consumption was lowest at ambient temperatures from 23–33 °C (Fig. 3). Within this thermoneutral zone (TNZ) the mean basal metabolic rate (BMR) was 0.34 ml $O_2/g \cdot h$, only 71 % of the mass-specific value calculated after the formula given by KLEIBER (1961).

Below $T_a = 23$ °C the oxygen uptake increased following the regression line: Y (ml $O_2/g \cdot h$) = $0.698 - 0.015T_a$ (°C) ($r = -0.84$); the increase was steeper in the male.

The minimal thermal conductance, as indicated by the slope of the regression line, was about 20 % below the expected value (as calculated after the formula of HERREID and KESSEL 1967). However, if corrected for changes in body temperature the overall conductance was about 25 % higher than expected at $T_a = 23$ °C, but decreased to the expected mass-specific level at $T_a = 10$ °C (Table 1).

Table 1

Dry thermal conductance $\left[C \text{ (ml } O_2/g \cdot h \cdot ^\circ\text{C)} = \frac{\dot{V}O_2 - E^*}{T_{re} - T_a} \right]$ at ambient temperatures from 23–10 °C

Figures in parentheses represent the relation of measured values to expected values after the formula of HERREID and KESSEL (1967)

T_a	(°C)	23	20	15	10
C	♂	0,024 (1,2)	0,024 (1,21)	0,022 (1,1)	0,021 (1,05)
	♀	0,024 (1,3)	0,025 (1,38)	0,022 (1,19)	0,019 (1,03)
	♂ + ♀	0,024 (1,25)	0,025 (1,31)	0,022 (1,14)	0,019 (1,03)

* E = evaporative heat loss

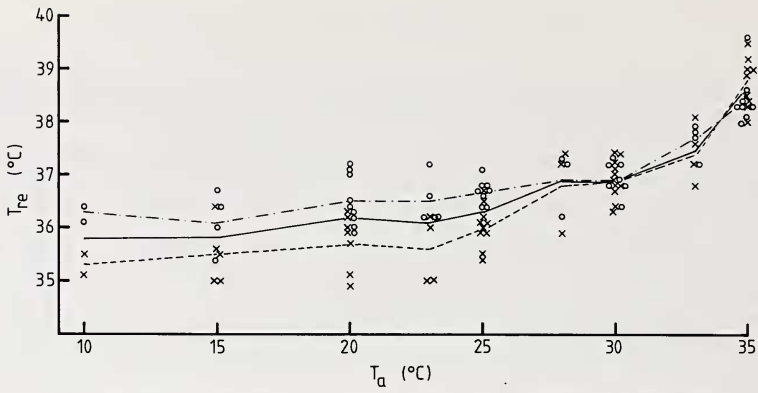


Fig. 2. Rectal temperatures after exposure to the various ambient temperatures. o = female; x = male; - - - - = mean values female; - · - · = mean values male; — = mean values of both animals

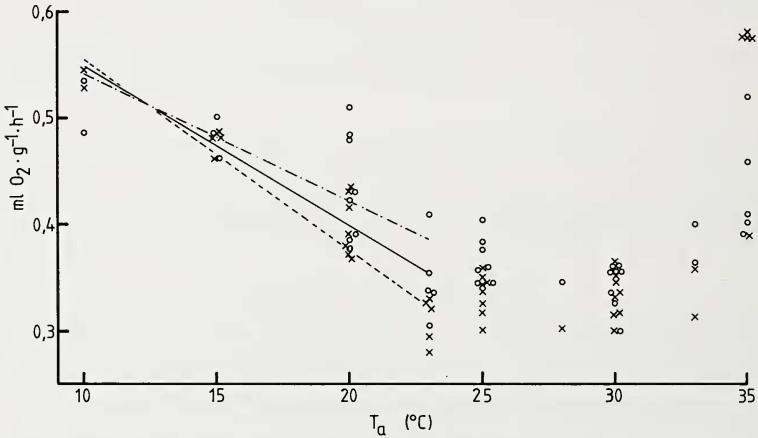


Fig. 3. Oxygen consumption during exposure to ambient temperatures from 10–35 °C. Indicated are also the regression lines below the thermoneutral zone. Same symbols as in Fig. 2

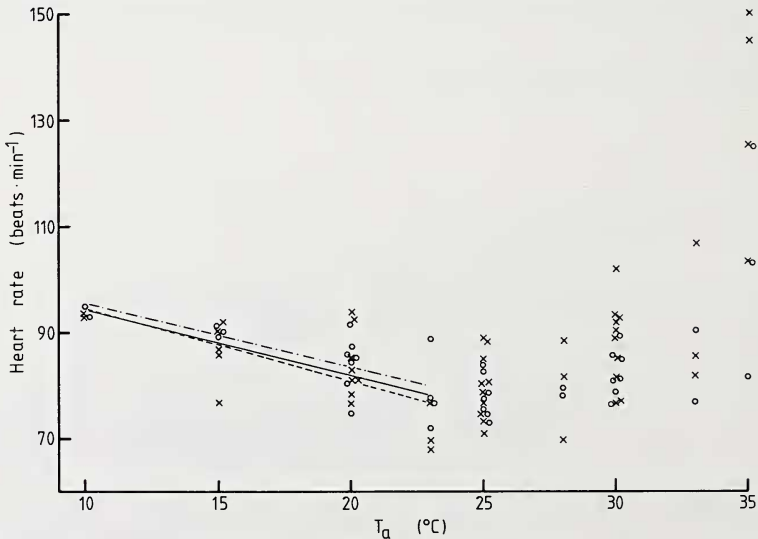


Fig. 4. Mean heart rates and regression lines at temperatures below the TNZ. Same symbols as in Fig. 2

Heart rate (HR) and oxygen pulse

Lowest mean heart rates were found at ambient temperatures from 23–28 °C with 75.5–79.4 beats/min (Fig. 4). If compared to the mass-specific value after the formula given by WANG and HUDSON (1971) this is only 66–70 % of the expected rate. During single experiments mean HR was lowest at $T_a = 23$ °C with 68 beats/min in the male.

Below the thermoneutral zone HR increased following the regression line: HR (beats/min) = $107 - 1.25T_a$ (°C) ($r = -0.68$). At high ambient temperatures mean HR gradually rose to 88 beats/min at $T_a = 33$ °C. At $T_a = 35$ °C HR largely depended on the state of the kinkajou: As long as the animals remained quiet HR was around 100 beats/min; however, when the animals got excited it increased to 130–150 beats/min.

In resting animals the mean oxygen transport per heart beat (= oxygen pulse) was lowest at temperatures from 28–35 °C with 170–182 $\mu\text{l}/\text{beat}$ (Fig. 5). At $T_a = 10$ °C the oxygen pulse rose to 245 $\mu\text{l}/\text{beat}$. Oxygen transport per heart beat was markedly lower in the male over the whole range of tested ambient temperatures.

Respiratory frequency (RF)

At ambient temperatures from 23–30 °C the mean respiratory frequency varied from 11.7–12.8 breaths/min (Fig. 6). At lower T_a 's it rose only slightly (to 15.7 breaths/min at $T_a = 10$ °C). At the upper end of the TNZ ($T_a = 33$ °C) the mean RF was 29 breaths/min; in a few cases it increased to about 60–80 breaths/min. At $T_a = 35$ °C RF gradually rose to 100–130 breaths/min within the first two hours of exposure. Thereafter it could remain within this range as long as the kinkajous were quiet. However, when the animals got excited, mean RF rose to above 200 breaths/min; maximal rates were found with 480 breaths/min. During heavy panting the mouth was opened, but the tongue was only slightly put out. Condensed water gathered around the nostrils and was licked up from time to time.

The simultaneous registration of breathing rates and rectal temperature by telemetry revealed that panting started when T_{re} had reached 37.5–38.1 °C; in the female this threshold temperature was slightly lower than in the male.

Total evaporative water loss (TEWL)

At ambient temperatures from 10–25 °C mean TEWL was 0.37–0.46 ml $\text{H}_2\text{O}/\text{kg}\cdot\text{h}$ (Fig. 7). It rose to 0.84 and 0.95 ml $\text{H}_2\text{O}/\text{kg}\cdot\text{h}$ at $T_2 = 33$ °C and $T_a = 35$ °C, respectively. During continuous panting the evaporation further increased to about 1.5 ml $\text{H}_2\text{O}/\text{kg}\cdot\text{h}$.

At $T_a = 33$ °C the dissipation of heat through evaporation amounted to about 30 % of the endogenous heat production (Fig. 8). The increased evaporation during panting at $T_a = 35$ °C did not improve this ratio due to the simultaneous rise of the oxygen uptake which led to an increased metabolic heat production.

Effects of different relative humidities (r.h.)

To find out about the effects of different water contents in the air entering the animal box, the kinkajous were exposed to relative humidities of 30 and 50 %, respectively, at ambient temperatures from 20–35 °C. Between 20–30 °C the different water content of the ingoing air did not markedly affect the measured parameters (Table 2). At $T_a = 35$ °C, however, the kinkajous showed signs of heat stress much earlier at r.h. = 50 %; heart rate and respiratory frequency were considerably higher than at r.h. = 30 %. Despite the increased breathing rate the dissipation of heat through evaporation was less at r.h. = 50 %, probably due to the higher water vapour pressure of the surrounding air. The effects were more pronounced in the male.

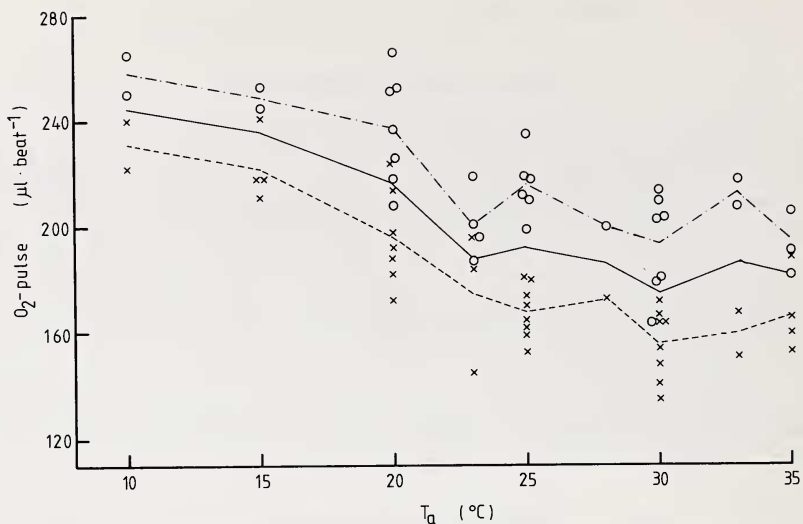


Fig. 5. Oxygen pulse during exposure to various ambient temperatures. Same symbols as in Fig. 2

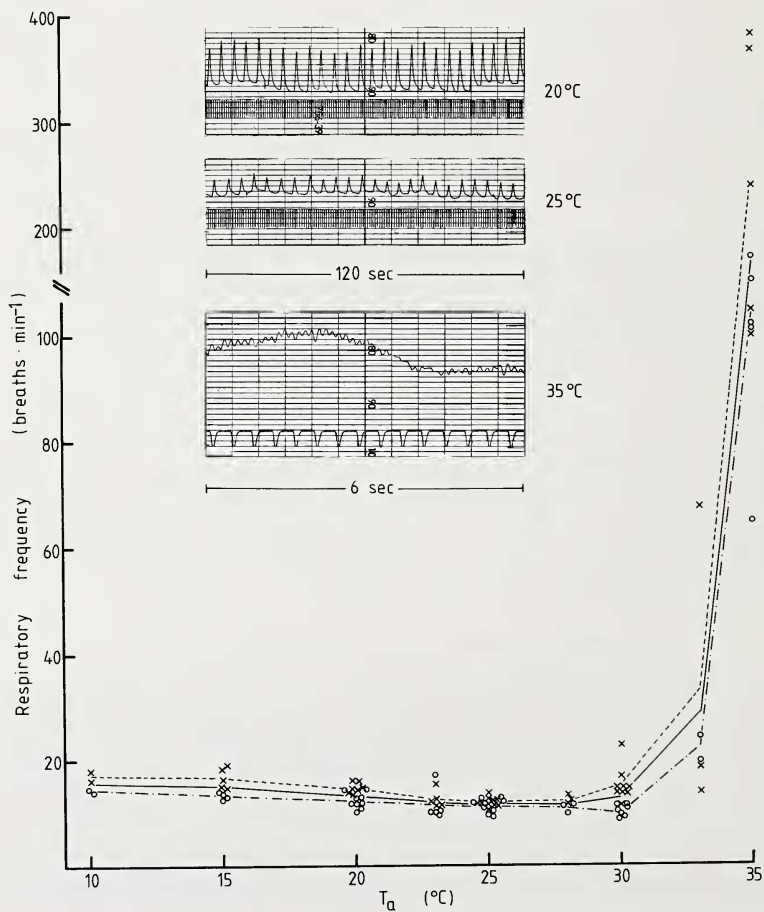


Fig. 6. Mean respiratory frequencies at ambient temperatures from 10–35 °C. Inserted are original registrations of respiration (upper curve) and heart rate (lower curve) at 20, 25 and 35 °C, showing respiratory arrhythmia of the heart beat pattern at 20 and 25 °C. Note that the ordinate scale is changed above 100 breaths/min. Same symbols as in Fig. 2

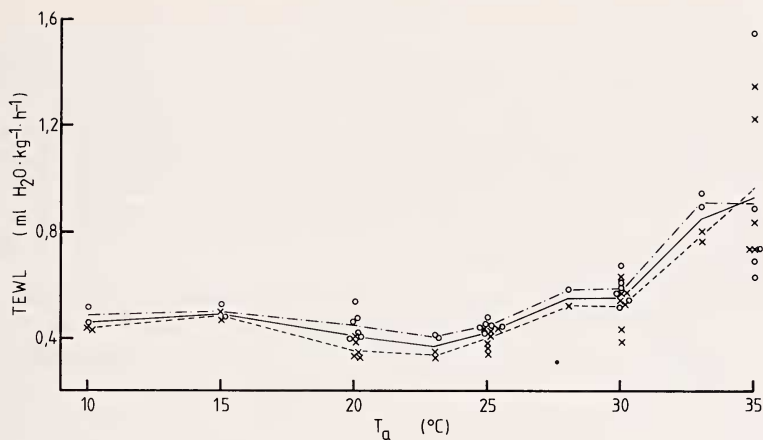


Fig. 7. Total evaporative water loss at ambient temperatures from 10–35 °C. Same symbols as in Fig. 2

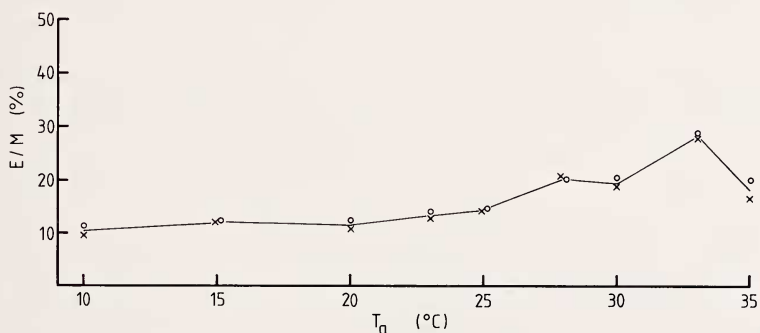


Fig. 8. Ratio of heat dissipation through evaporative pathways (E) to metabolic heat production (M). Same symbols as in Fig. 2

Table 2

Effects of different relative humidities in the air entering the animal box on rectal temperature (T_{re}), oxygen consumption ($\dot{V}O_2$), total evaporative water loss (TEWL), heart rate (HR) and respiratory frequency (RF) at ambient temperatures (T_a) from 20–35 °C

Mean values from two experiments with each animal at any temperature/humidity combination

T_a (°C)	r. h. (%)	T_{re} (°C)	$\dot{V}O_2$ (ml/g · h)	TEWL (ml H ₂ O/kg · h)	HR (min ⁻¹)	RF (min ⁻¹)
20	30	36,5	0,466	0,432	84,9	14,7
	50	36,2	0,406	0,378	89,7	13,2
25	30	36,4	0,347	0,424	81,5	10,8
	50	36,5	0,359	0,4	83,8	12,6
30	30	37,2	0,357	0,557	84,3	12
	50	36,9	0,346	0,463	88,8	13,5
35	30	38,6	0,453	0,887	92,4	144,5
	50	38,7	0,492	0,714	125,3	256,6

Discussion

Our results on the regulation of body temperature and oxygen consumption of kinkajous confirm previous reports that the basal metabolic rate in this species is reduced to 65–70 % of the mass-specific value (MÜLLER and KULZER 1977; McNAB 1978). When exposed to ambient temperatures from 10–33 °C the rectal temperature is regulated within 35–38 °C. At $T_a = 35$ °C, however, the kinkajous often get excited, although not yet being in a true hyperthermic state: In most cases, when the experiments had to be stopped, T_{re} was below 39 °C, which is still within the normal range of body temperature during the nocturnal activity (MÜLLER and KULZER 1977).

The closely related coatis (*Nasua nasua*) endure heat-exposure much better: In this species T_{re} usually did not exceed 38 °C after 5–6 hours at $T_a = 35$ °C (CHEVILLARD-HUGOT et al. 1980). In one coati T_{re} had risen to 39 °C only after 5 hours at $T_a = 37$ °C; however, measuring of T_{re} by telemetry revealed a slow but steady rise of the body temperature. It can be supposed that the greater heat tolerance of the coatis is an adaptation to their daily mode of life by which they are regularly exposed to direct sunshine.

Within the thermoneutral zone the mean basal heart rate of the kinkajous was found to be slightly higher than that of coatis (75–80 beats/min vs 67.5–72.5 beats/min). On a mass-specific basis this is in both species only 66–70 % of the expected rate (calculated after the formula of WANG and HUDSON 1971). The reduction of the basal metabolic rate, however, is more pronounced in the coatis: 60 % vs 70 % of the theoretical value in the kinkajous (CHEVILLARD-HUGOT et al. 1980; this study). In the kinkajous the oxygen pulse within the TNZ is smaller than in the coatis (175 vs 245 $\mu\text{l}/\text{beat}$); a direct comparison of the two procyonid species is difficult because of their different body size. An allometric equation relating oxygen pulse to body size has not yet been developed. If compared to other mammals it seems that the oxygen pulse of the kinkajous is relatively high: In springhares (*Pedetes capensis*), for example, which are only slightly smaller and have a similarly reduced BMR, the oxygen pulse at thermoneutrality was measured with 140 $\mu\text{l}/\text{beat}$ (MÜLLER et al. 1979). However, it is unclear why the lively coatis should have a relatively smaller capacity for oxygen transport in blood than kinkajous.

Up to now only few investigations have dealt with respiratory frequencies of mammals during sleep. Most values cited in the literature were recorded from quiet but awake animals. The allometric equation for a mass-specific breathing rate given by STAHL (1967) is probably also largely based upon such data. Following this equation the kinkajous should have a mean resting breathing rate of almost 42 breaths/min. In our experiments we found a mean of only about 12 breaths/min during sleep and at thermoneutrality. KRUMBIEGEL (1953) reports a much higher breathing rate in this species: 47 breaths/min. The only slight rise of the respiratory frequency in a cold environment (to 15.7 breaths/min at $T_a = 10$ °C) suggests that the higher oxygen uptake was mainly achieved by increasing the tidal volume.

At ambient temperatures above 30 °C the kinkajous markedly accelerated their breathing rate. Panting, however, started only when the body temperature had reached a threshold value between 37.5–38.1 °C. Visual observation revealed that the first panting phase always coincided with an awaking of the animals. In the fennec, a desert-dwelling carnivore, BANHOLZER (1974) found panting threshold temperatures between 38.8–39.4 °C. Panting did not contribute to increase the ratio of dissipated heat versus endogenous heat production. Together with the acceleration of the breathing rate – and the thereby increased evaporation – the oxygen consumption of the kinkajous also rose markedly, thus leading to an unfavourable situation: If compared to $T_a = 33$ °C, where about 30 % of the metabolic heat production could be dissipated by evaporative means, at $T_a = 35$ °C this ratio was only about 20 %. The fennec is able to increase its heat loss by evaporation from about 35 % of the metabolic heat load at $T_a = 32$ °C to about 55 % (mean value) at $T_a = 38$ °C (NOLL-BANHOLZER 1979).

It such seems that kinkajous, although being able to pant vigorously (with maximal frequencies up to 480 breaths/min), cannot increase evaporation as effectively as is known from other carnivores. The following points might be important in this regard: 1. Differently from other carnivores kinkajous open the mouth only slightly during panting and the tongue is hardly put out. 2. The shape of the tongue also differs from most other carnivores; it is very long and narrow, such presumably diminishing the effective surface area for evaporation. 3. If compared to fennecs, the body temperature as well as the threshold temperature at which panting starts is about 1.5 °C lower. This means that in kinkajous the exhaled air which passes the respiratory surfaces has a lower temperature than in fennecs and thus can absorb less water. 4. Possibly the panting frequency of kinkajous does not show the energetically favourable accordance with the resonant frequency of the respiratory system as was found e.g. in dogs and pigeons (CRAWFORD 1962; CRAWFORD and KAMPE 1971). This might partly explain for the detrimental increase of the internal heat production during panting which exceeds the enhanced dissipation of heat.

From our results it can be concluded that kinkajous are well adapted to the rather stable temperature conditions in the middle-jungle of neotropical rain forests. Their abilities for physiological temperature regulation suffice to prevent hyperthermia as long as ambient temperatures do not exceed 33 °C, which is probably rarely the case. Sleeping in shaded places and the nocturnal activity help to avoid the adverse effects of direct sunshine. If T_a exceeds 33 °C and the body temperature rises, an alarming system with a rather low threshold temperature guarantees that the kinkajous wake up early enough to change to places with more favourable conditions. The ability, on the other hand, to dissipate heat through evaporative pathways is limited. This, however, seems to be reasonable as in their habitat the water vapour pressure of the air is usually high and would minimize the effectiveness of evaporative cooling.

Zusammenfassung

Atemfrequenz, pulmocutane Wasserabgabe und Herzfrequenz beim Wickelbären (Potos flavus Schreber)

Am Wickelbären wurden Herzfrequenz, Atemfrequenz und pulmocutane Wasserabgabe untersucht. Bei Umgebungstemperaturen von 10–33 °C konnte die Rektaltemperatur im Bereich 35,8–37,3 °C reguliert werden; bei 35 °C Umgebungstemperatur stieg sie auf 38,6 °C. Der Sauerstoffverbrauch war im Bereich von 23–33 °C am niedrigsten. Hier betrug der Basalstoffwechsel 0,34 ml O₂/g·h; das sind nur 71 % des gewichtsspezifischen Erwartungswertes. Bei Temperaturen unterhalb der thermischen Neutralzone erhöhte sich der O₂-Verbrauch nach der Regressionsgleichung: Y (ml O₂/g·h) = 0,698 - 0,015T_a (°C). Die mittlere Ruheherzfrequenz war am niedrigsten zwischen 23–28 °C mit 78 Schlägen/min; die niedrigsten Werte wurden bei 23 °C gemessen mit 68 Schlägen/min. Der mittlere Sauerstoffpuls lag bei Temperaturen von 28–35 °C bei 170–182 µl/Herzschlag; bei 10 °C stieg er auf 245 µl/Herzschlag. Zwischen 23–30 °C lag die mittlere Atemfrequenz während des Schlafes bei 12 Atemzügen/min. Niedrigere Temperaturen führten nur zu einem geringen Anstieg. Bei 33 °C erhöhte sich die Atemfrequenz auf 29–30 Atemzüge/min, und bei 35 °C setzte Hecheln ein, wenn die Rektaltemperatur einen Schwellenwert zwischen 37,5–38,1 °C erreicht hatte. Die maximale Hechelfrequenz betrug 480 Atemzüge/min. Die pulmocutane Wasserabgabe betrug 0,37–0,46 ml/kg·h bei Temperaturen von 10–25 °C. Während anhaltenden Hechelns stieg sie auf etwa 1,5 ml/kg·h. Die Wärmeabgabe durch Verdunstungskühlung war jedoch niedrig: Bei 33 °C wurden nur etwa 30 % der körpereigenen Wärmeproduktion durch Verdunstung abgegeben, und dieser Anteil wurde während des Hechelns noch geringer, da gleichzeitig der Sauerstoffverbrauch deutlich anstieg.

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Age determination, reproduction, and mortality of the Gray fox (*Urocyon cinereoargenteus*) in Maryland, U.S.A.¹

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Abstract

Four techniques for determining age were investigated for 143 gray foxes (*Urocyon cinereoargenteus*) collected in Maryland, 1976–1979: 1. counts of cementum layers in the teeth, 2. epiphyseal closure of the humerus, 3. eye lens weights and 4. baculum length and weight. Age distribution analyses indicated a balanced age structure. The juvenile segment of the population exceeded 50% in each of the three seasons studied. The overall sex ratio for Maryland gray foxes was 123.4 males per 100 females. Mean testis weights and spermatogenic activity suggested that adult male gray foxes become fertile sooner than juveniles entering their first mating season. The onset of estrus in female gray foxes from Maryland appeared to occur in early February. Mean litter size, estimated from placental scar counts, was 4.42 (range 3–5) pups per year. The prenatal mortality rate was estimated to be 39% and the implantation rate of ova was 88%. The proportion of barren females was 45%.

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